 0030-0950/82/0005-0282 $2.00/0

SELECTIVE OCCURRENCE OF ARBORESCENT SPECIES ON SOILS IN A DRAINAGE TOPOSEQUENCE, OTTAWA COUNTY, OHIO[1]

ERNEST S. HAMILTON, Department of Biological Sciences, Bowling Green State University, Bowling Green, OH 43403.

ARTHUR LIMBIRD, Department of Geography, University of Calgary, Calgary, Alberta, Canada T2N 1N4

ABSTRACT The arborescent species composition of a woodlot on the southern shore of Western Lake Erie is described using the analysis of data collected from a series of quadrats located throughout the woodlot. The range of tolerance to edaphic moisture conditions for selected species, in particular *Fraxinus pennsylvanica,* and *Fraxinus pennsylvanica var. subintegerrima,* indicates a range of habitat conditions under which individual species are competitively successful. Two soils, a somewhat poorly drained Nappanee silt loam and a very poorly drained Toledo silty clay vary in several of the chemical properties analyzed as well as in moisture status and thus influence soil moisture availability, aeration, and nutrient availability. These soils seem to play a key role in maintaining 2 distinct arborescent community types within this woodlot.

OHIO J. SCI. 82(5): 282, 1982

INTRODUCTION

The plant communities growing along the southern shore of the western Lake Erie basin generally have received only cursory treatment in the literature. These studies include only general descriptions (Gordon 1966, 1969; Kaatz 1955) of habitat and species present. The only quantitative descriptions of community types describes arborescent species composition in relation to 2 soil types (Hamilton and Limbird 1979). Except for this study, only general information is available describing the soils along the lake shore (Paschall et al. 1928, Ohio DNR 1974, Ohio DNR 1981). The present study further correlates arborescent species distribution in relation to moisture regimes determined by 2 distinct soils.

STUDY SITE

The Ottawa National Wildlife Refuge is located in Benton Township, Ottawa County at latitude 41°37′N and longitude 83°14′W. The specific area, designated as Ottawa Woods, is located within the Refuge in the NE quarter of section 34, township 8N, range 14E. It is bounded on the north and east by Crane Creek and associated marshes of the Lake Erie shore, and on the south and west by flat, low agricultural fields. The total hardwood forest encompasses about 3 ha of which 1.8 ha are included in this study. The general area is nearly flat and poorly drained glacial lake plain approximately 175 m above sea level.

The mesic, humid climate of the study area is directly influenced by the close proximity of Lake Erie, which provides for moderation of seasonal extremes and a somewhat longer growing season than away from the Lake (Preston 1975). The climatic parameters for the southern lake shore in this general location have previously been enumerated and are similar to those of the Davis-Besse nuclear plant site about 18 km east (Hamilton and Limbird 1979).

[1]Manuscript received 28 May 1981 and in revised form 21 December 1981 (#81-23).

The substrate consists of 2 general soils developed in a lacustrine deposit of the proglacial lake, Nappanee silt loam, fine, illitic, mesic aeric Ochraqualf and Toledo silty clay, fine, illitic, nonacid, mesic mollic Haplaquept. The parent material of the Nappanee soil is moderately fine fresh water sediments, one meter thick and underlain by glacial till, while the Toledo soil has developed in fine fresh water sediments. The poorly drained soils generally are similar in appearance and morphology except for the color and prominent mottling resulting from very poor drainage in the Toledo soil. The soils differ only slightly in physiography; the Nappanee soil occupies nearly imperceptable rises in the landscape, while the Toledo soil occupies slight depressions. Thus, it is a drainage toposequence difference in soils that is being investigated; other soil forming factors, macroclimate, time, parent material, and organisms available for colonizations are similar for the 2 soils (Jenny 1980).

METHODS AND MATERIALS

A soil sampling station was established in a representative soil area in each of the Nappanee silt loam and the Toledo silty clay in summer 1976. The soils were identified and soil profiles were described (table 1). Bouyoucos gypsum soil blocks were calibrated using pressure plate extraction of moisture at ⅓, 5, 10, and 15 atm and then buried at 10, 20, and 50 cm depths in the A_1, A_2, and B_2 horizons of each soil. Percent available moisture by weight was determined weekly with a Bouyoucos Model BN-2B moisture meter and summarized on a monthly basis to facilitate interpretation of differences between the 2 soils. Soil temperatures were recorded on previously calibrated remote recording thermographs in each of the 3 horizons for both soils, and summarized using weekly mean minimum, mean maxi-

TABLE 1

Soil profile descriptions, Ottawa Woods, Ottawa National Wildlife Refuge, Ottawa County, Ohio.

Horizon	Depth cm	Description
Nappanee Silt Loam		
A_1	0-16	Dark grayish brown (10YR 4/2) silt loam; moderate, medium crumb; friable; abundant roots; gradual, smooth boundary; pH 6.3.
A_2	16-24	Dark gray (10YR 4/3) silt loam; weak, fine platy to weak, fine crumb; friable; few roots; clear, smooth boundary; pH 6.2.
B_1	24-34	Brown (10YR 5/3) silty clay loam; common, fine, faint yellowish brown (10YR 5/4) mottles; moderate, subangular blocky; firm; clear, smooth boundary; pH 6.4.
B_{2t}	34-104	Light yellowish brown (10YR 6/4) silty clay; common, fine distinct grayish brown (10YR 5/2) mottles; strong subangular blocky; very firm; gradual, smooth boundary; pH 6.4.
B_3	104-112	Light yellowish brown (10YR 6/4) with gray (5Y 6/1) and reddish brown (5YR 4/3) common, medium, prominent mottles; silty clay loam; moderate, subangular blocky; abrupt, wavy boundary; pH 6.8.
11C	112+	Light yellowish brown (10YR 6/4); clay loam glacial till; strong, medium angular, blocky; calcareous; pH 7.2.
Toledo Silty Clay		
A_1	0-18	Dark to very dark grayish brown (10YR 3/2); silty clay; moderate, fine crumb; firm to friable; gradual, smooth boundary; pH 6.3.
A_2	18-30	Dark gray (10YR 4/3) silty clay; few, fine, distinct yellowish brown (10YR 5/6) mottles, weak, fine subangular blocky; firm; clear, smooth boundary; pH 6.0.
B_{1g}	30-44	Brownish gray (2.5Y 4/2) with dark gray (5Y 4.5/1) common, medium, prominent mottles; silty clay; moderate, medium subangular blocky; firm; gradual, wavy boundary; pH 6.0.
B_{2g}	44-94	Light brownish gray (2.5Y 6/2); silty clay; strong, medium angular blocky; very firm; gradual, smooth boundary; pH 5.9.
B_{3g}	94-100	Light brownish gray (2.5Y 6/2); silty clay loam; moderate, medium angular blocky; firm; abrupt, smooth boundary; pH 6.4.
C	100+	Light brownish gray (2.5Y 6/2); clay loam; massive; calcareous; pH 7.0.

mum, and average values from hourly readings for comparison with moisture availability and length of growing season.

Soil chemical analyses were carried out by an independent soil testing laboratory to prevent biased results. Chemical analyses were based on composite samples taken from each of the 2 soils in the A_1, A_2, and B_2 horizons where instruments for soil moisture and soil temperature had been installed. Soil pH was determined in a 0.01M $CaCl_2$ solution (Peech 1965). Cation exchange capacity and exchangeable cations of Ca, Mg, K, Na were determined in a 1N solution of (NH_4OAc) at pH 7.0 (Chapman 1965). Sulfates were determined colorimetrically using 0.1 $MCaCl_2$ (Johnson and Nishita 1952, Dean 1966). Organic matter was determined by the wet combustion, colorimetric method (Sims and Haby 1971). Phosphorus was determined as $NaHCO_3$ soluble P (Olsen and Dean 1965). The values of chemical soil constituents were tested for significance using a Chi-square test at the 0.05 level of significance.

Investigation of the woody plant species of Ottawa Woods was initiated in the spring of 1977. A permanent study area 180 × 100 m in size was established using 1.5-m steel fence posts spaced 20 m apart, so that a grid system was constructed encompassing 180 permanet 10 × 10 m quadrats in the central, least disturbed portion of the woods.

The vegetation was sampled using nested quadrats. Within 10 × 10 m quadrats, arborescent species more than 2.54 cm DBH (diameter at breast height) were recorded by species and DBH. Individuals less than 2.54 cm DBH but more than 3.0 m tall were tallied by species only. The sapling and shrub layer (composed of woody species more than 30 cm but less than 3.0 m in height) was sampled in 4 × 4 m quadrats located in the northwest corners of the larger quadrats. In these, the number of individual saplings and shrubs was counted by species. The number of woody seedlings (those woody individuals less than 30 cm tall) was recorded by species in 0.5 × 2 m quadrats placed in the northwest corners of the 4 × 4 m quadrats. Nomenclature of all species follows that of Fernald (1950).

Calculation of importance values was done by modification of the Curtis and McIntosh (1951) and Buell et al. (1966) methods as described by Hamilton and Forsyth (1972). They were obtained by totaling the relative overstory values for density, frequency, and dominance, and dividing this total by 3. The importance values for all other species considered in the remaining vegetational layers were obtained by dividing the sum of the relative values of density and frequency by 2. Thus, values are comparable in all the vegetational layers sampled, with the maximum importance value in any one layer being equal to 100.

RESULTS AND DISCUSSION

The characteristics of the 2 soils of the study area indicate that they are quite similar except for their moisture regimes due to the microrelief differences between rises and depressions in the near level landscape and the effects of moisture on other soil properties (table 2). Organic matter content, and milliequivalents per 100 g (me/100g) of calcium, magnesium, potas-

TABLE 2

Average soil analysis values, Ottawa Woods, Ottawa National Wildlife Refuge, Ottawa County, Ohio.

	Nappanee Soil			Toledo Soil		
Horizon Property	A_1	A_2	B_{2t}	A_1	A_2	B_{2g}
pH	6.28	6.20	6.42*	6.28	6.02	5.95*
CEC	24.4	23.4	21.8*	25.6	24.9	25.4*
% base sat.	84.5	86.0	93.6*	83.9	81.1	86.2*
% Ca sat.	60.4	58.0	57.4†	60.7	52.6	51.1†
% Mg sat.	21.6	25.5	33.8	20.7	26.1	32.9
H (me/100g)	4.0	3.8	1.7*	4.1	5.0	3.6*
Ca (me/100g)	14.5	13.1	12.2	15.6	12.8	12.7
Mg (me/100g)	5.1	5.7	7.2	5.2	6.4	8.3
K (me/100g)	0.6	0.6	0.5	0.6	0.6	0.6
Na (me/100g)	0.2	0.2	0.2	0.1	0.1	0.2
ppm sulfates	22	18*	25*	24	30*	41*
ppm P	24	19	8	32	17	10
% organic matter	6.9	3.8	1.7	6.6	3.8	1.9

*Significant at 0.05 level.
†Significant at 0.10 level.

TABLE 3

Soil particle size analysis, Ottawa Woods, Ottawa National Wildlife Refuge, Ottawa County, Ohio.

Nappanee Soil				Toledo Soil			
Horizon	Sand	Silt	Clay	Horizon	Sand	Silt	Clay
A_1	26.0*	52.2	21.8*	A_1	9.6*	47.9	42.5*
A_2	23.6*	51.6	24.8*	A_2	9.2*	44.5	46.3*
B_1	18.7*	50.1	31.2*	B_{1g}	8.8*	44.1	47.1*
B_{2t}	15.3*	45.3	39.4*	B_{2g}	8.6*	43.5	47.9*

*Difference significant at 0.05 level.

sium, sodium, and phosphorus are not significantly different between the Nappanee and Toledo soils. It is only at depth that differences in soil properties become apparent. The very poorly drained characteristic of the Toledo soil is indicated by gleying (g) in the B_{1g}, B_{2g}, B_{3g} horizons compared to the Nappanee soil (table 1). The g subscript is an indication of the presence of reduced iron in the soil as a result of water being present in the profile for extended periods of time. Gleying and the accompanying reduction conditions in the absence of adequate oxygen results in greater accumulations of forms of sulfur in the Toledo soil. Significantly greater accumulations of sulfates in the A_2 and B_{2g} horizons of the Toledo soil as compared to the Nappanee soil are due to the significantly greater amount of clay in the Toledo soil (table 3) and the sulfate retention ability of the clay (Tisdale and Nelso 1975). The increase in hydrogen cations normally associated with reduction conditions, results in a significantly lower pH in the B_{2g} horizon of the Toledo soil than the B_{2t} horizon of the Nappanee soil.

Cation exchange capacity (CEC) is significantly higher in the B_{2g} horizon of the Toledo soil than in the B_{2t} horizon of the Nappanee soil because of the significantly higher clay content in the Toledo soil (table 3). However, percent base saturation and percent Ca saturation are significantly lower in the Toledo soil than in the Nappanee soil due to the substitution of hydrogen ions for bases in the Toledo soil. Thus, higher moisture levels in the Toledo soil affect soil characteristics that induce differences in plant community composition beyond the direct influence of moisture availability.

TABLE 4

Average monthly moisture values (% available by weight) Nappanee and Toledo soils, Ottawa Woods, Ottawa National Wildlife Refuge, Ottawa County, Ohio.

	Nappanee Soil			Toledo Soil		
Month*/horizon	A_1	A_2	B_{2t}	A_1	A_2	B_{2g}
March	87.5	87.3	90.8	94.7	94.5	96.7
April	97.2	98.5	100.0	98.9	99.4	100.0
May	93.6	87.8	100.0	100.0	100.0	100.0
June	90.7	79.8	98.1	99.4	99.5†	100.0
July	58.0†	31.6†	68.0†	73.8†	76.0†	83.9†
August	43.1†	42.4†	49.8†	59.1†	62.9†	65.1†
September	42.8	51.6	52.6†	56.2	61.8	72.6†
October	43.9†	60.9	48.1†	59.5†	49.8	70.8†
November	64.1†	69.6	55.3	77.4†	61.1	66.8

*Averages have not been included for December, January, and February because the soil usually has been frozen, creating inaccurate moisture availability values.

†Significance at 0.05 level.

Differences in the moisture regimes of the Toledo and Nappanee soils can be demonstrated only partially using moisture availability data (table 4). Available moisture is the moisture in the soil between field capacity (.33 atm) and wilting point (15 atm). A summary of moisture values indicates that the Toledo soil is slower to dry out in spring and usually re-establishes higher moisture levels earlier than the Nappanee soil. In addition, soil moisture generally does not drop as low in the Toledo soil. Not all of the monthly average values were statistically significant. However, water normally ponds on the surface of the Toledo soil areas in spring making the topographic expression of the slight rises of the Nappanee soil areas visible. The Nappanee soil areas have not been ponded in 5 springs of observation in Ottawa Woods.

The wetter Toledo soil warms more slowly in spring at all 3 depths monitored.

TABLE 5

Importance values of species in Ottawa Woods, Ottawa National Wildlife Refuge, Ottawa County, Ohio.

	Tree Layer	Shrub & Sapling Layer	Seedling Layer
Fraxinus pennsylvanica	10.89	4.45	1.71
Fraxinus pennsylvanica var. *subintegerrima*	10.65	16.59	5.28
Carya ovata	9.81	1.05	0.14
Quercus rubra	8.00	2.26	1.05
Crataegus sp.	7.77	2.23	2.77
Tilia americana	7.76	8.03	0.43
Quercus alba	7.05	0.29	0.25
Cornus amomum	5.74	7.40	2.42
Cornus drummondi	4.95	15.44	6.26
Quercus bicolor	4.78	0.23	0.25
Carya cordiformis	3.62	0.75	0.43
Acer saccharinum	3.10	5.90	0.28
Ulmus rubra	3.09	1.75	0.68
Quercus macrocarpa	2.80	0.00	0.00
Quercus palustris	1.67	0.00	0.00
Carpinus caroliniana	1.34	0.29	0.40
Viburnum lentago	1.28	1.76	0.57
Viburnum prunifolium	1.05	2.12	0.49
Corylus americana	0.95	2.99	0.25
Lindera benzoin	0.68	1.03	1.39
Acer rubrum	0.61	1.57	0.25
Prunus virginiana	0.56	1.08	0.14
Ostrya virginiana	0.50	0.29	0.14
Cornus obliqua	0.39	6.33	2.75
Rosa sp.	0.31	3.33	0.85
Sambucus canadensis	0.14	0.00	0.00
Gymnocladus dioica	0.12	0.00	0.00
Xanthoxylum americanum	0.08	1.03	0.17
Fraxinus nigra	0.07	0.15	0.00
Acer negundo	0.06	0.15	0.00
Euonymus atropurpureus	0.06	0.00	0.00
Fraxinus americana	0.06	0.00	0.00
Celtis occidentalis	0.04	0.00	0.14
Fraxinus quadrangulata	0.04	0.00	0.00
Vitis sp.	0.00	2.86	12.42
Ribes americana	0.00	7.33	3.53
Rubus sp.	0.00	1.09	0.46
Populus deltoides	0.00	0.29	0.00
Rhus radicans	0.00	0.00	49.16
Parthenocissus quinquefolia	0.00	0.00	4.96

The growing season is effectively shortened by the significantly cooler soil temperatures. A 40 F value was used as a measure of the potential growing season of the root environment of the arborescent species. The average number of days with soil temperatures 40 F for the A_1 horizons is 206 for the Toledo soil compared to 221 for the Nappanee soil; for the A_2 horizons 206.5 compared to 228; and for the B_2 horizons 208 compared to 230. Each of these differences are significant at a 0.10 level. Thus, higher soil moisture levels in the Toledo soil reduce soil temperatures so that the growing season is shortened by about 20 days. This may especially delay germination of seeds and growth of seedlings in the spring.

Ottawa Woods can be described as a *Fraxinus pennsylvanica, F. pennsylvanica* var. *subintegerrima, Carya ovata,* and *Quercus rubra* community (table 5). Together these 4 species provide better than 39% of the total importance value of the tree layer. A second group of 3 arborescent species, *Crataegus* sp., *Tilia americana,* and *Quercus alba* account for more than 22% of the importance value, while a third group of 6 species *Quercus bicolor, Carya cordiformis, Acer saccharinum, Ulmus rubra, Q. macrocarpa,* and *Q. palustris* contribute slightly more than 19% of the total importance value of the tree layer. The 4 canopy species, *Fraxinus pennsylvanica* var. *subintegerrima, F. pennsylvanica, Acer saccharinum,* and *Tilia americana,* with a total importance value of about 35% are most important in the sapling layer. In addition, 3 shrub species, *Cornus drummondi, C. amomum,* and *C. obliqua,* contribute slightly more than 29% importance value to this layer. The reproductive layer is dominated by *Rhus radicans* with an importance value slightly less than 50% followed by *Vitis* sp. at slightly over 12%. Arborescent reproduction is dominated by *Fraxinus pennsylvanica* var. *subintegerrima* and shrub reproduction by *Cornus drummondi.*

The arborescent species composition of Ottawa Woods strongly suggests that it should be classified as transitional phase 3 of the Elm-Ash-Soft Maple community of Sampson (1930). This Red Oak-Linden transition is characterized by *Fraxinus pennsylvanica* (Red ash), *F. pennsylvanica* var. *subintegerrima* (Green ash), *Carya ovata, C. cordiformis, Quercus rubra, Tilia americana,* and *Ulmus rubra.* These 7 species account for almost 54% of the total importance value of the tree layer and approximately 64% of the importance value of the true canopy species present. Although importance values in the sapling layer (34.88%) and seedling layer (9.72%) are somewhat low, comparison made between the true arborescent species increases these values dramatically. These canopy species contribute 73.66% and 63.84% of the importance values of the potential canopy individuals present in the sapling and seedling layers, respectively.

The range of species present in the 3 vegetational layers indicates a range of moisture tolerance, from very poorly drained (including standing water) to somewhat poorly drained soil habitats. Figure 1 depicts this moisture gradient using selected species. It is based on our own observations of the habitat occurrence of these species as well as habitat preferences cited by Braun (1961), Fernald (1950), Gleason and Cronquist (1963), Hosie (1973), Otis (1931), and Stava (1978). The range of tolerance to edaphic moisture conditions for these selected species indicates a wide range of habitat conditions in this community. Direct observation also indicates that these species seem to be distributed in the community in relationship to the slight differences in microtopography. These appeared to be controlled by variation in soils in a toposequence and result in heterogeneous soil moisture conditions throughout the woods as discussed above.

With these variables in focus, soil types were mapped, and specific quadrats located entirely in areas underlain by these 2 soils were selected for further study. This included 46 nested quadrats situated entirely within the Toledo soil and 106 located within the Nappanee soil. The tree data from these selected quadrats were ana-

TABLE 6

Tree data for the Toledo and Nappanee soils of Ottawa Woods, Ottawa National Wildlife Refuge, Ottawa County, Ohio.

	Nappanee Soil								Toledo soil							
	Total Stems per Hectare	Total Basal Area per Hectare	Density	Fre-quency	Domi-nance	Relative Density	Relative Fre-quency	Relative Domi-nance	Total Stems per Hectare	Total Basal Area per Hectare	Density	Fre-quency	Domi-nance	Relative Density	Relative Fre-quency	Relative domi-nance
Fraxinus pennsylvanica	87*	6650.7*	0.87*	48.11*	66.51*	3.27	6.21	15.95	602*	8220.9*	6.02*	78.26*	82.21*	27.31	11.73	20.45
Fraxinus pennsylvanica var. *subintegerrima*	640*	2383.7*	6.40*	72.64*	23.84*	24.04	9.38	5.72	126*	1347.9*	1.26*	34.78*	13.48*	5.72	5.21	3.35
Carya ovata	212	2649.0	2.12	84.91	26.49	7.96	10.96	6.35	198	3621.2	1.98	71.74	36.21	8.98	10.75	9.01
Quercus rubra	109*	9639.7*	1.09	59.43	96.40*	4.10	7.67	23.12	28*	1048.7*	0.28	23.91	10.49*	1.27	3.58	2.61
Crataegus sp.	354*	1470.3*	3.54	83.96	14.70*	13.30	10.84	3.53	128*	530.4*	1.28	52.17	5.30*	5.81	7.82	1.32
Tilia americana	220	3181.9*	2.20	71.70	31.82*	8.27	9.26	7.63	154	1348.5*	1.54	54.35	13.49*	6.99	8.14	3.36
Quercus alba	40*	11206.5*	0.40	32.08*	112.02*	1.50	4.14	26.86	0*	0.0*	0.00	0.00	0.00*	0.00	0.00	0.00
Cornus amomum	293*	65.5*	2.93	7.19*	0.65	11.01	7.19	0.16	117	17.4	1.17	39.13	0.17	5.31	5.86	0.04
Cornus drummondi	229	77.6	2.29	43.40	0.78	8.60	5.60	0.19	176	65.1	1.76	41.30	0.65	7.99	6.19	0.16
Quercus bicolor	9*	2044.7	0.09	6.60	20.45	0.34	0.85	4.90	33*	11872.6*	0.33	26.09	118.73*	1.50	3.91	29.53
Carya cordiformis	92	561.8	0.92	54.72	5.62	3.46	7.07	1.35	70	787.3	0.70	28.26	7.09	3.18	4.23	1.76
Acer saccharinum	70*	84.6	0.28	28.30	0.85	1.05	3.65	0.20	183*	1082.7*	1.83	45.65	10.84*	8.30	6.84	2.70
Ulmus rubra	47*	165.0	0.47	29.25	1.65	1.77	3.78	0.40	154*	999.7*	1.54	52.17	10.00*	6.99	7.82	2.49
Quercus macrocarpa	3	894.4	0.03	2.83	8.94	0.11	0.37	2.14	7	3732.2*	0.07	6.52	37.32*	0.32	0.98	9.28
Quercus palustris	1	216.7	0.01	0.94	2.17	0.04	0.12	0.52	15*	5506.6*	0.15	13.04	55.07*	0.68	1.95	13.70
Carpinus caroliniana	69*	209.0	0.69	13.21	2.09	2.59	1.71	0.50	30*	95.3	0.30	30.44	0.95	1.36	4.56	0.24
Viburnum lentago	52	12.0	0.52	13.21	0.12	1.95	1.71	0.03	24	—	0.24	10.87	—	1.09	1.63	—
Viburnum prunifolium	59*	28.2	0.59	18.85	0.28	2.22	2.44	0.07	7*	—	0.07	4.35	—	0.32	0.65	—
Corylus americana	51*	1.5	0.51	13.21	0.01	1.92	1.71	0.002	0*	0.0	0.00	0.00	0.00	0.00	0.00	0.00
Lindera benzoin	19	3.7	0.19	6.60	0.04	0.72	0.85	0.01	22	3.4	0.22	4.35	0.03	1.00	0.65	0.01
Acer rubrum	5*	0.9	0.05	5.66	0.01	0.19	0.73	0.002	24*	—	0.24	15.22	—	1.19	2.28	—
Prunus virginiana	5*	4.8	0.05	3.77	0.05	0.19	0.49	0.01	61*	—	0.61	10.87	—	2.77	1.63	—
Ostrya virginiana	18*	63.8	0.18	9.43	0.64	0.68	1.22	0.15	4*	—	0.04	4.35	—	0.18	0.65	—

Cornus obliqua	4	—	0.04	2.83	—	0.15	0.37	—	13	—	0.13	8.70	—	0.59	1.30	—
Rosa sp.	3	—	0.03	2.83	—	0.11	0.37	—	15	—	0.15	6.52	—	0.68	0.98	—
Sambucus canadensis	3	—	0.03	1.89	—	0.11	0.24	—	2	—	0.02	2.17	—	0.09	0.33	—
Fraxinus nigra	0*	0.0	0.00	0.00	0.00	0.00	0.00	0.00	11*	—	0.11	2.17	—	0.50	0.33	—
Gymnocladus dioica	2	40.9	0.02	1.89	0.45	0.08	0.24	0.11								
Xanthoxylum americanum	2	—	0.02	0.94	—	0.08	0.12	—								
Acer negundo	1	—	0.01	0.94	—	0.04	0.12	—								
Euonymus atropurpureus	2	—	0.02	1.89	—	0.08	0.24	—								
Fraxinus americana	1	40.6	0.01	0.94	0.41	0.04	0.12	0.01								
Celtis occidentalis	1	40.3	0.01	0.94	0.04	0.04	0.12	0.01								
Fraxinus quadrangulata	1	—	0.01	0.94	—	0.04	0.12	—								

*Significant at 0.05 level.

lyzed using the Chi-square test. Results indicated 2 distinct arborescent communities related to differences in soil properties previously discussed (table 6). The number of individuals and density values for *Fraxinus pennsylvanica* were approximately 7 times greater in the Toledo soil than in Nappanee soil. Basal area and dominance values for individuals of *Quercus bicolor* and *Ulmus rubra* in the wetter Toledo soil were approximately 6 times greater than values on the Nappanee soil. Much greater differences in these values were exhibited for *Acer saccharinum* (13X) and *Quercus palustris* (25X). *Quercus macrocarpa* also has significantly greater basal area and dominance values in the Toledo soil. In contrast, the number of individuals and density values for *Fraxinus pennsylvanica* var. *subintegerrima* were 5 times greater in the Nappanee soil than in the Toledo soil and *Quercus alba* was confined to the Nappanee soil. Basal area and dominance values were 3 times greater for *Crataegus* sp. and 9 times greater for *Quercus rubra* in the Nappanee soil. Basal area and dominance values were also significantly greater in the Nappanee soil for *Tilia americana*.

Differences in species composition and community structure in relation to distribution of 2 soils has been previously documented in an area designated as the Tower Woods that is only 13 km east of the present study area (Hamilton and Limbird 1979). The 2 soils supported distinct communities that were in an earlier successional stage than the Ottawa Woods. Nevertheless, the same general concepts of species response to habitat variations that act to separate one species population from another are valid (Bell 1974, Collinson 1977, Del Moral 1972, Hamilton and Limbird 1979, Morison et al. 1948, Zimmerman and Wagner 1979).

To evaluate further these later successional communities in relation to the 2 soils, importance values were calculated for all species occurring in association with each soil type (table 7). In the true canopy

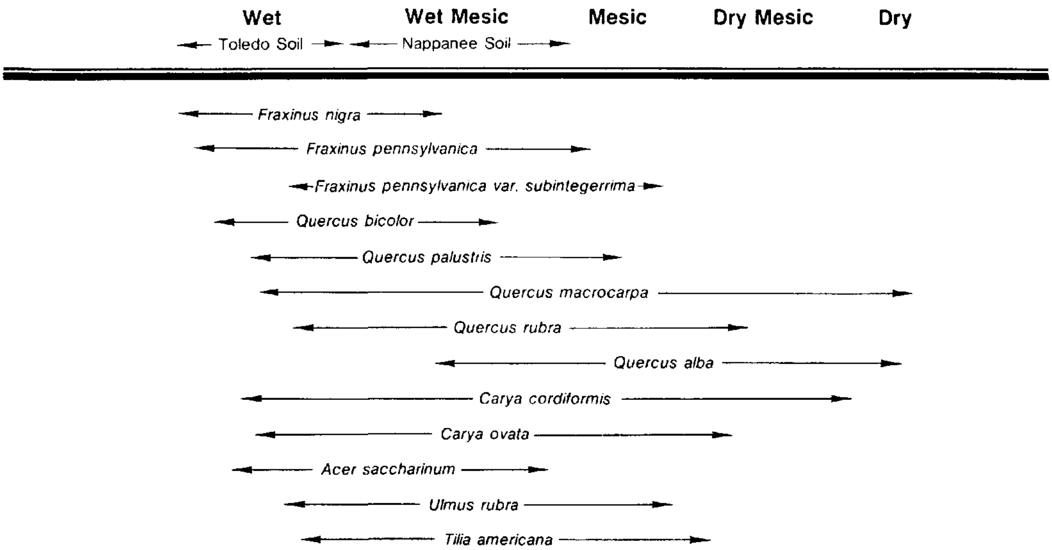

FIGURE 1. Moisture gradients of important arborescent species in Ottawa Woods, Ottawa County, Ohio.

layer, differences in importance values proved to be significant between soils for 11 species. Four species, *Fraxinus pennsylvanica* var. *subintegerrima, Quercus rubra, Q. alba* and *Crataegus* sp. were significantly more important in the areas of Nappanee soil. Seven species, *Fraxinus pennsylvanica, Quercus bicolor, Acer saccharinum, Ulmus rubra, Q. palustris, Q. macrocarpa,* and *F. nigra,* were significantly more important in the areas of Toledo soil. In the shrub and sapling layer, *Fraxinus pennsylvanica* var. *subintegerrima, Crataegus* sp., *Tilia americana, Carya cordiformis, Viburnum prunifolium,* and *Corylus americana* were more important in areas of Nappanee soil, while *Fraxinus pennsylvanica, F. nigra, Acer saccharinum, ·Populus deltoides, Cornus obliqua,* and *Viburnum lentago* were more important in areas of Toledo soil.

In the seedling layer, *Fraxinus pennsylvanica* var. *subintegerrima, Rhus radicans,* and *Parthenocissus quinquefolia* were more important in the Nappanee soil. In the Toledo soil, *Fraxinus pennsylvanica, Ulmus rubra, Cornus drummondi, C. obliqua,* and *Vitis* sp. were more important. Overall, the species most diagnostic in all three vegetational layers appear to be *Fraxinus pennsylvanica* var. *subintegerrima* in areas of the somewhat poorly drained Nappanee soil and *F. pennsylvanica* in areas of the very poorly drained Toledo soil.

The response of various species to yearly moisture regimes in the 2 soils undoubtedly is related to soil aeration and nutrient availability and uptake (Hamilton and Limbird 1979) which manifests itself through competition. Higher moisture content of the Toledo soil in both fall and spring (table 4), coupled with spring ponding and subsequent delayed drying, inhibits many species (Morison et al. 1948, Wilde 1958). Delayed drying and higher moisture content effectively shorten the growing season as the Toledo soil remains cooler longer in spring and cools sooner in fall compared to the Nappanee soil. The inhibiting effect of high moisture levels on nutrient uptake has been well documented (Kellman 1975, Kramer and Kozlowski 1960, Voigt 1958), with different species evolving differing tolerances to the lack of aeration and nutrients (Brown and Curtis 1952, Morison et al. 1948).

The ranges of tolerance for selected arborescent and shrub species are depicted in fig. 1. Obviously these overlap, with certain species exhibiting very wide ranges of tolerance to moisture while others are highly restricted. The significantly important arborescent species in the very wet Toledo soil, particularly *Fraxinus pennsylvanica, Acer saccharinum, Ulmus rubra, Quercus palustris, Q. macrocarpa,* and *Q. bicolor,* are better adapted to excess moisture and reduced nutrient absorption than other species such as *Quercus rubra, Q. alba,* and

TABLE 7

Importance values of the different woody species in the Nappanee and Toledo soils in Ottawa Woods, Ottawa National Wildlife Refuge, Ottawa County, Ohio.

	Nappanee Soil			Toledo Soil		
	Tree Layer	Shrub and Sapling Layer	Seedling Layer	Tree Layer	Shrub and Sapling Layer	Seedling Layer
Fraxinus pennsylvanica	8.48*	2.14*	1.24*	19.83*	14.19*	5.42*
Fraxinus pennsylvanica var. *subintegerrima*	13.05*	17.68*	6.73*	4.76*	10.25*	2.33*
Carya ovata	8.42	1.05	0.20	9.58	1.32	0.00
Quercus rubra	11.63*	2.72	0.81	2.49*	1.60	2.33
Crataegus sp.	9.22+	3.27*	3.20	4.94+	0.00*	4.02
Tilia americana	8.39	9.96*	0.66	6.16	3.11*	0.00
Quercus alba	10.83*	0.48	0.40	0.00*	0.00	0.00
Cornus amomum	6.12	8.95	2.46	3.74	7.80	2.88
Cornus drummondi	4.80	14.49	4.35*	4.78	17.19	14.14*
Quercus bicolor	2.03*	0.13	0.20	11.65*	0.00	0.00
Carya cordiformis	3.96	1.24+	0.44	3.06	0.00+	0.00
Acer saccharinum	1.63*	5.16+	0.20	5.95*	9.77+	0.00
Ulmus rubra	1.98*	2.08	0.40	5.77*	1.60	2.76+
Quercus macrocarpa	0.87+	0.00	0.00	3.55+	0.00	0.00
Quercus palustris	0.23*	0.00	0.00	5.41*	0.00	0.00
Carpinus caroliniana	1.60	0.40	0.42	2.05	0.00	0.74
Viburnum lentago	1.23	1.30+	0.20	0.91	3.77+	1.28
Viburnum prunifolium	1.58	3.09*	0.51	0.32	0.00*	0.96
Corylus americana	1.21+	4.37*	0.40	0.00+	0.00*	0.00
Lindera benzoin	0.53	0.77	1.26	0.55	0.66	2.55
Acer rubrum	0.31	1.42	0.20	1.12	2.45	0.74
Prunus virginiana	0.23	0.19	—	1.47	1.13	—
Ostrya virginiana	0.68	0.48	—	0.28	—	0.74
Cornus obliqua	0.17	3.71*	1.08*	0.63	9.22*	5.51*
Rosa sp.	0.16	2.24	0.88	0.55	2.45	1.81
Sambucus canadensis	0.12	—	—	0.14	—	—
Gymnocladus dioica	0.14	—	—	—	—	—
Xanthoxylum americanum	0.07	1.06	0.24	—	0.85	—
Fraxinus nigra	0.00+	0.00+	—	0.28+	0.66+	—
Acer negundo	0.05	—	—	0.00	—	—
Euonymus atropurpureus	0.11	—	—	0.00	—	—
Fraxinus americana	0.09	—	—	0.00	—	—
Celtis occidentalis	0.06	—	0.20	0.00	—	—
Fraxinus quadrangulata	0.05	—	—	0.00	—	—
Vitis sp.	—	1.90	6.78*	—	3.95	39.21*
Ribes americana	—	8.19	3.17	—	6.11	3.50
Rubus sp.	—	1.50	0.71	—	0.66	0.00
Rhus radicans	—	—	57.01*	—	—	7.65
Parthenocissus quinquefolia	—	—	5.87*	—	—	1.49
Populus deltoides	—	0.00+	—	—	1.32+	—

*Significant at 0.01 Level.
+Significant at 0.05 Level.

Crataegus sp. which tend to be more prevalent on the better drained Nappanee soil. The 2 distinct community types occupying these 2 soils thus are regulated by differences in soil moisture, which affect aeration, availability of nutrients, and pH values and thus restrict or enhance survival effects of species having different moisture tolerances.

LITERATURE CITED

Bell, D. T. 1974 Tree stratus composition and distribution in the stream-side forest. Amer. Midl. Nat. 92: 35-46.

Braun, E. L. 1961 The woody plants of Ohio. Ohio State Univ. Press, Columbus. 362 p.

Brown, R. T. and J. T. Curtis 1952 The upland conifer-hardwood forests of northern Wisconsin. Ecol. Mono. 22: 217-234.

Buell, M. F., A. N. Langford, D. W. Davidson and L. F. Ohmann 1966 The upland forest continuum in northern New Jersey. Ecology 47: 416-432.

Chapman, H. D. 1965 Cation exchange capacity. *In:* C. A. Block (ed.). Methods of Soil Analysis Part 2. p. 891-901.

Collinson, A. S. 1977. Introduction to world vegetation. George Allen and Unwin, London, England. 201 p.

Curtis, J. T. and R. P. McIntosh 1951 An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32: 476-496.

Dean, G. A. 1966 A simple Coloumetric finish for the Johnson-Nishita micro-distillation of sulfur. Analyst 9: 530-532.

Del Moral, R. 1972 Diversity patterns in forest vegetation of the Wenatchee Mountains, Washington. Bull Torrey Bot. Club 99: 57-64.

Fernald, M. L. 1950 Gray's manual of botany, 8th Ed. Amer. Book Co., Philadelphia, PA. 596 p.

Gleason, H. A. and A. Cronquist 1963 Manual of vascular plants of northeastern United States and adjacent Canada. D. Van Nostrand Co., Inc., Princeton, N. J. 810 p.

Gordon, R. B. 1966 Natural vegetation of Ohio at the time of the earliest surveys. Ohio Biol. Surv. (map).

——— 1969 The natural vegetation of Ohio in pioneer days. Ohio Biol. Surv., U. S. 3 (2). 109 p.

Hamilton, E. S. and J. L. Forsyth 1972 Forest communities of South Bass Island, Ohio. Ohio J. Sci. 72: 189-210.

Hamilton, E. S. and A. Limbird 1979 Soil types and arborescent species of a specific woodlot in Ottawa County, Ohio. Ohio J. Sci. 79: 195-203.

Hosie, R. C. 1973 Native trees of Canada. Canadian Forestry Service, Dep. Environ., Ottawa. 380 p.

Jenny, H. 1980 The soil resource. Springer-Verlag, NY. Chap. 11: 276-304.

Johnson, C. M. and H. Nishita 1952 Microestimation of sulfur in plant materials, soils, and irrigation waters. Anal. Chem. 24: 736-742.

Kaatz, M. R. 1955 The black swamp: A study in historical geography. Ann. Assoc. Amer. Geog. 55: 1-35.

Kellman, M. C. 1975 Plant geography. Methuen and Co. Ltd., London, England. 135 p.

Kramer, D. J. and T. T. Koslowski 1960 Physiology of trees. McGraw-Hill, NY. 642 p.

Morison, G. T., A. C. Hoyle and J. R. Hope-Simpson 1948 Tropical soil-vegetation catenas and mosaics. J. Ecol. 36: 1-84.

Ohio Department of Natural Resources 1974 Soil map of Ottawa County, Div. Lands and Soil, Columbus.

Ohio Department of Natural Resources 1981 An inventory of Ohio soils, Ottawa County, Div. Lands and Soil, Columbus.

Olsen, S. R. and L. A. Dean 1965 Phosphorous. *In:* C. A. Black, (ed.). Methods of soil analysis. Part 2. p. 1035-1049. Agronomy #9. Amer. Soc. Agron. Madison, WI.

Otis, C. H. 1931 Michigan trees. Univ. of Mich. Press, Ann Arbor. 362 p.

Paschall, A. H., J. G. Steele and G. W. Conrey 1928 Soil survey of Ottawa County, Ohio. U. S. D. A. Bureau of Chem. and Soils, Series 1928, No. 26, 38 p. and map.

Peech, M. 1965 Hydrogen-ion activity *In:* C. A. Black (ed.). Methods of soil analysis Part 2; p. 914-926.

Preston, D. E. 1975 Natural history and vascular flora list of Davis-Besse Nuclear Power Plant Property. Unpubl. MS thesis, Bowling Green State Univ., Bowling Green, OH. 71 p.

Sampson, H. C. 1930 Succession in the swamp forest formation in northern Ohio. Ohio J. Sci. 30: 304-357.

Sims, J. R. and V. A. Haby 1971 Simplified colorimetric determination of soil organic matter. Soil Sci. 112: 137-141.

Stava, P. S. 1978 Handbook of trees for the Midwest. Kendall/Hunt Pub. Co., Dubuque, IA. 324 p.

Tisdale, S. L. and W. L. Nelson 1975 Soil fertility and fertilizer, 3rd ed. MacMillan Co., NY. Chap. 8.

Voigt, G. K. 1958 Plant-soil factors in soil chemical analysis. First North Amer. Forest Soils Conf. 31-41.

Wilde, S. A. 1958 Forest soils. The Ronald Press, NY. 537 p.

Zimmerman, M. and W. L. Wagner 1979 A description of the woody vegetation of oak-hickory forest in the Northern Ozark Highlands. Bull. Torrey Bot. Club 106: 117-122.